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7. Review of Bats of the Endemic Antillean Genus *Monophyllus*

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As recently as 1959, Hall and Kelson (p. 116) commented on the status of the bats comprising the seven species of the phyllostomatid genus *Monophyllus*, endemic to the Antillean region: "Some of the species of *Monophyllus* are known from only one specimen and none is really well represented in collections. Therefore the extent and nature of individual variation is only poorly known. Further, the characters employed to distinguish each of the several species from others are minor differences in proportion that are best appreciated only by direct comparison." Consequently, Hall and Kelson's key to the named species of *Monophyllus* is based primarily on provenance of the known kinds rather than on morphological characteristics; such a course could hardly have been avoided since nowhere are there definitive statements concerning the variation of all the species involved. Miller, the first and only reviser (1900) of *Monophyllus*, had at that time eight specimens. From

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this suite of material he named three new species, one of which was from an unknown locality. Between 1900 and the present, additional material has accumulated, but, aside from occasional large series from specific localities, the accretion has been gradual; material from the Lesser Antilles has been especially slow in reaching collections.

The field work of the senior author has taken him to all islands whence *Monophyllus* has been reported although he has not in every case secured specimens. In his Antillean endeavors, Schwartz has had the assistance of Ronald F. Klinikowski, David C. Leber, and Richard Thomas; all have made collections of *Monophyllus* that have interest and value. The junior author spent six weeks on Dominica in 1966 under the auspices of the Bredin-Archbold-Smithsonian Biological Survey of Dominica and secured the first recent series of *Monophyllus* from any of the Lesser Antillean islands.

Eight names are currently associated with the genus *Monophyllus* Leach, as follows: *M. redmani* Leach, 1821 (type-species); *M. portoricensis* Miller, 1900; *M. plethodon* Miller, 1900; *M. clinedaphus* Miller, 1900; *M. cubanus* Miller, 1902; *M. luciae* Miller, 1902; *M. frater* Anthony, 1917; *M. ferreus* Miller, 1918. Of these, all but *M. c. cubanus* and *M. c. ferreus* are regarded as full species; *M. frater* is known only from fossil fragments and *M. clinedaphus* is known from a single specimen of unknown provenance. The ranges of the species, as presently understood, are: *M. redmani*, Jamaica; *M. portoricensis*, Puerto Rico; *M. plethodon*, Barbados; *M. cubanus cubanus*, Cuba; *M. c. ferreus*, Hispaniola; *M. luciae*, St. Lucia; *M. frater*, Puerto Rico, fossil; *M. clinedaphus*, unknown.

Both of us have collected specimens of *Monophyllus* on the Lesser Antillean island of Dominica. In borrowing specimens from various collections, we have inadvertently discovered unreported *Monophyllus* from several other Lesser Antillean islands. Although it was not our intent to examine all specimens of *Monophyllus* presently available, we have been able to study a total of 139 specimens from throughout the West Indies. Abbreviations used in the present paper to denote collections in which *Monophyllus* are housed are: AMNH (American Museum of Natural History); AS (Albert Schwartz collection); BMNH (British Museum, Natural History, London); KU (Museum of Natural History, University of Kansas); MCZ (Museum of Comparative Zoology, Harvard University); RMNH (Rijksmuseum van Natuurlijke Historie, Leiden); USNM (United States National Museum). For the loan of material we are grateful to Karl F. Koopman, John E. Hill, Miss Barbara Lawrence, A. M. Husson, and Charles O. Handley, Jr. The senior author also wishes to acknowledge the gift of specimens of Cuban *Monophyllus* from Gilberto Silva Taboada.

Gary L. Ranck has supplied us with invaluable data on two of the holotypes in the United States National Museum.

All external measurements and weights, except for length of forearm, are those recorded by the collectors on original labels. Skull measurements and length of forearm were taken with vernier calipers; all are standard and expressed in millimeters. Length of maxillary tooththrow is the alveolar length and greatest length of skull includes upper incisors. All weights are given in grams.

### Systematic Treatment

Six nominal forms of *Monophyllus* (excluding for the moment *M. frater* and *M. clinedaphus* from consideration) vary in total length from a low mean of 61 (Hispaniola) to a high mean of 78 (Dominica), with the Jamaican population almost as large (mean 76) as the Dominican specimens, and the Cuban and Puerto Rican material almost as small (means 66 and 65) as the Hispaniolan bats. In general, other external measurements follow this same trend; means for length of forearm range from 36.9 on Puerto Rico to 42.1 on Dominica and St. Lucia. Cranial measurements likewise show the same tendencies; greatest length of skull varies from 19.0 (Puerto Rico) to 24.2 (Dominica), with means from 19.9 (Puerto Rico) to 23.4 (Dominica). Length of maxillary tooththrow ranges from 6.8 (Puerto Rico) to 8.9 (Jamaica), with means from 7.1 (Puerto Rico) to 8.5 (Jamaica). Cranial measurements generally form a continuum (with Puerto Rican bats having the smallest skulls and Lesser Antillean or Jamaican bats having the largest) and are useful primarily at the subspecific level. Several cranial features, however, suggest that we are dealing with two species rather than one as would otherwise seem to be the case.

One of the characters that was presumed to separate the Barbadian *M. plethodon* from its relatives was the fact that the two upper premolars (PM 2 and PM 3 in formal terminology) were so crowded that the customary diastema between these two teeth was obliterated. Comparison of a skull of *M. plethodon* with those of *Monophyllus* from the Leeward and Windward Islands shows that this feature is common to all Lesser Antillean specimens in that the space between the upper premolars is narrow, much less than half the length of the first tooth. On the other hand, this space in Greater Antillean *Monophyllus* is long, being at least as long as half the length of the first premolar, and often longer. We have been unable to determine any other wholly consistent cranial or dental details and have placed emphasis on this relatively trivial feature as a basis for distinguishing two species (rather than six) among the living *Monophyllus*. We are deterred from considering all *Monophyllus* as conspecific by the

knowledge that at one time *M. portoricensis* and *M. frater* were contemporaneous on Puerto Rico. *Monophyllus portoricensis* has a long diastema (like other Greater Antillean forms) and *M. frater* has a short one (like the Lesser Antillean assemblage). Thus, Puerto Rico is interpreted as once having been inhabited by two stocks of *Monophyllus*, one Greater Antillean and the other Lesser Antillean, of which the latter is presumed presently to be extinct.

Once this dichotomy is recognized, the two species can be shown to differ in some average cranial measurements. Greatest length of skull in Greater Antillean bats varies from 19.0 to 23.9, for example, whereas that of Lesser Antillean bats ranges from 21.4 to 24.2. Post-orbital constriction shows almost no overlap, with Greater Antillean *Monophyllus* having measurements of 3.8 to 4.6 and Lesser Antillean specimens having measurements of 4.5 to 5.0. Less trenchant differences include length of forearm (35.5 to 42.8 in Greater Antilles, 38.8 to 45.7 in Lesser Antilles). Although facial adornments have been gainfully employed to distinguish between congeneric species of other genera of phyllostomatids, the noseleaves and chin details in all *Monophyllus* appear identical. It is possible that we are over-emphasizing the single dental character between the two species and that they are indeed preferably considered as conspecific, but such an action tends to obscure the one major difference between the two geographic segments of *Monophyllus*. It also poses the problem of the relationships of *M. frater*, which would then have to be regarded as a local derivative of *M. portoricensis* on Puerto Rico—a derivative oddly like its Lesser Antillean congeners—or else double invasion of the island by widely different stocks of the same species would need to be postulated. We feel that our arrangement is defensible zoogeographically as well as morphologically and provides a more meaningful systematic arrangement than that currently in use.

### *Monophyllus* Leach

*Monophyllus* Leach, 1821, p. 75. [Generotype: *Monophyllus redmani* Leach.]

#### *Monophyllus redmani* Leach

DEFINITION.—A species of *Monophyllus* characterized by a combination of small to large size (total length 58–80), small hind foot (9–14), small ear (ear from notch 9–14), short forearm (35.5–42.8), small skull (greatest length 19.0–23.9), narrow postorbital constriction (3.8–4.6), and the upper premolars separated by a diastema one-half or more the length of the first premolar. The pelage is some shade of brown, tending generally toward paler shades.

Key to Living Species and Subspecies of Genus *Monophyllus*

1. Upper premolars separated by diastema equal to one-half or more of length of first premolar . . . . . 2  
Upper premolars crowded, separated by small diastema less than half length of first premolar . . . . . 4
2. Maxillary tooththrow more than 7.5 mm. . . . . 3  
Maxillary tooththrow less than 7.4 mm. . . . . *M. r. portoricensis*
3. Greatest length of skull 22.8 mm or more. . . . . *M. r. redmani*  
Greatest length of skull 22.4 mm or less . . . . . *M. r. clinedaphus*
4. Forearm shorter (38.8–41.0 mm); maxillary tooththrow shorter (7.2–7.8 mm).  
Forearm longer (40.1–45.7 mm); maxillary tooththrow longer (7.8–8.5 mm).  
*M. p. plethodon*  
*M. p. luciae*

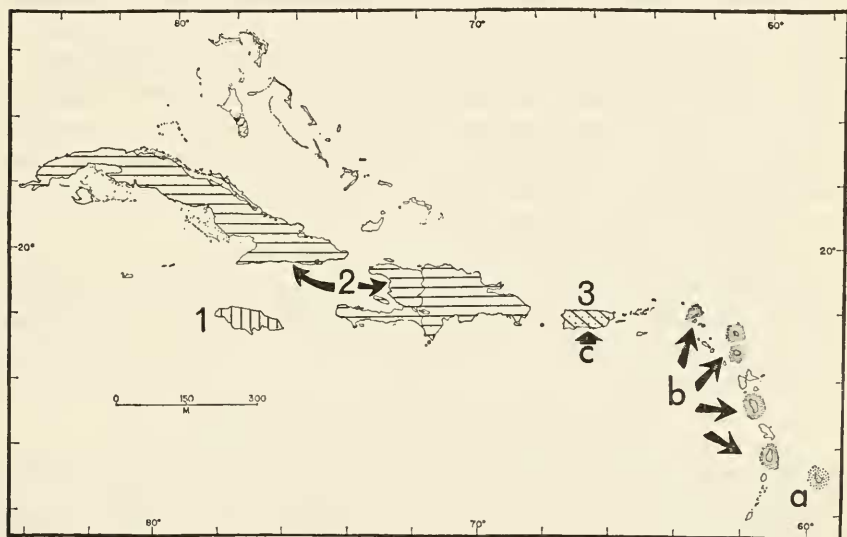


FIGURE 1.—Distribution of *Monophyllus* in the West Indies (*M. redmani*=lines; *M. plethodon*=stippling): 1, *M. r. redmani* (vertical lines); 2, *M. r. clinedaphus* (horizontal); 3, *M. r. portoricensis* (diagonal); a, *M. p. plethodon* (heavy stippling); b, *M. p. luciae* (medium); c, *M. p. frater* (open).

*Monophyllus redmani redmani* Leach

*Monophyllus redmani* Leach, 1821, p. 76. [Type-locality: Jamaica.]

DISTRIBUTION.—Known only from Jamaica (see fig. 1).

DEFINITION.—A subspecies of *M. redmani* characterized by large body size (total length 73–80, mean 76.1) but relatively short forearm (37.6–41.0, mean 40.2), large skull (greatest length 22.8–23.9, mean 23.3) with broad postorbital and mastoid regions and zygomata, and long tooththrow. The color varies from dark brown to pale brown; there is no obvious dichromatism.

REMARKS.—*Monophyllus r. redmani* is the largest subspecies of the species and is readily separable from other subspecies by the



greatest length of skull (lower extreme in *M. r. redmani* 22.8, high extreme in all other subspecies 22.4). Other skull measurements (condylobasal length, postorbital constriction, mastoidal breadth) show some degree of overlap but length of maxillary tooththrow (8.3–8.9 in *M. r. redmani*, 6.8–8.3 in other races) is almost as effective as greatest length of skull in distinguishing the nominate subspecies. Of external measurements, the total length of *M. r. redmani* is greater (73–80) than that of the other two subspecies (59–71), and measurements of ear from notch lie at the upper extreme for the species. Mensural data are given in tables 1 and 2.

The senior author took four specimens of *M. r. redmani* from a large cave at Windsor, Jamaica, where the bats were observed clinging to and flying just below the high ceiling of the moist cave, well back from the entrance. Koopman and Williams (1951, p. 20) recorded *Monophyllus* in surface and subsurface deposits in Jamaican caves, but not as fossils: these authors regarded *M. redmani* as common in Jamaica today (p. 23). Williams (1952) reported *Monophyllus* from the "bat layers" of a single cave at Portland. No information has been published on weights or dates of parturition.

**SPECIMENS EXAMINED.**—JAMAICA: St. Elizabeth Parish: Oxford Cave, Balaclava, 2 ♂, 3 ♀ (AMNH 45233, 45236–39). Trelawny Parish: Windsor, 3 ♂, 2 ♀ (AMNH 45241–42, 45244–46); Windsor Cave, 3 ♂, 1 ♀ (AS 5248–51); no specific locality, other than Jamaica, 1 ♂ (MCZ 45778).

#### *Monophyllus redmani clinedaphus* Miller

*Monophyllus clinedaphus* Miller, 1900, p. 36. [Type-locality: unknown, herein restricted to the vicinity of Baracoa, Oriente Province, Cuba.]

*Monophyllus cubanus* Miller, 1902, p. 410. [Type-locality: Baracoa, Oriente Province, Cuba.]

*Monophyllus cubanus ferreus* Miller, 1918, p. 40. [Type-locality: cave eight miles west-southwest of Jérémie, Département du Sud, Haiti.]

**DISTRIBUTION.**—Cuba and Hispaniola; on the latter island apparently as yet unknown in the Dominican Republic (see fig. 1).

**DEFINITION.**—A subspecies of *M. redmani* characterized by small body size (total length 59–70, mean 65.5 for six Cuban specimens and 60.7 for three Hispaniolan specimens), relatively long forearm (37.6–42.5, mean 40.1 for 32 Cuban specimens and 39.8 for 24 Hispaniolan specimens), skull of moderate size (greatest length 21.0–22.1, mean 21.9 for nine Cuban specimens and also for four Hispaniolan specimens) with broad postorbital region, moderately broad mastoid region, and narrow zygomata, and moderately long tooththrows. The color is brownish, generally paler than in *M. r. redmani*.

**REMARKS.**—*Monophyllus clinedaphus* was described by Miller (1900, p. 36) on the basis of a single male in alcohol with skull re-

moved. The major difference between *M. clinedaphus* and the other "species" recognized in the same paper—*M. redmani*, *M. portoricensis*, *M. plethodon*—was that the "plane of the basioccipital and basisphenoid, instead of sloping forward at a faint angle as in the other species of the genus, pitches abruptly forward and downward at an angle of 32°." It may be recalled also that Miller had no material at that time from Cuba or Hispaniola and, thus, was unaware of the size and general characters of populations from those islands.

Gary L. Ranck (pers. comm., Feb. 8, 1966) has taken measurements for us of the skull and skin of the holotype (USNM 5210/37405) of *M. clinedaphus*. Pertinent measurements are: forearm 39.6; greatest length of skull 21.7, condylobasal length 19.6, postorbital constriction 4.1, maxillary tooththrow 7.8. Ranck also confirmed the peculiarity of the basioccipital-presphenoid angle on which Miller placed so much emphasis, but Ranck suggested (as had C. O. Handley previously) that it may well be due to the fact that the skull was removed from a specimen in spirits and that preparation and subsequent drying possibly resulted in distortion of the skull. Later, the junior author examined the skull of *M. clinedaphus* and reached a similar conclusion, i.e., that it somehow had been distorted after collection. The base of the braincase, just above the basioccipital-presphenoid angle, clearly indicates that the skull has been bent, probably while wet and, therefore, possibly prior to the time it was extracted for study. Additionally, the palate is damaged, having been laterally compressed so that the toothrows are closer together than usual and nearly parallel. In any event, in all measurements except condylobasal length the holotype of *M. clinedaphus* agrees with *Monophyllus* examined from Cuba (the condylobasal length in the holotype is 19.6, whereas the lowest measurement in nine Cuban bats is 19.7). In the maxillary tooththrow, the first two premolars are separated by a diastema slightly more than half the length of the first tooth, indicating that the holotype presumably originated in the Greater Antilles. We have seen no other specimen, however, with the peculiar basioccipital-presphenoid configuration of *M. clinedaphus* and conclude that this unique condition is indeed due to distortion. Therefore, we consider *M. clinedaphus* as the prior name for those bats that up to now have been known as *Monophyllus cubanus* Miller, 1902.

Mensural data for the two segments of *M. r. clinedaphus* are presented in tables 1 and 2. Of the three subspecies of *M. redmani*, the Cuban and Hispaniolan *M. r. clinedaphus* is intermediate in size between *M. r. redmani* of Jamaica and *M. r. portoricensis* of Puerto Rico. This is demonstrated most clearly by cranial measurements. Forearms of *M. r. redmani* and *M. r. clinedaphus* are comparable in size; thus, the forearms are relatively longer in *M. r. clinedaphus* than in

*M. r. redmani* since the former is otherwise a larger bat than the latter. *Monophyllus r. clinedaphus* can be separated completely from *M. r. redmani* on the basis of greatest length of skull; the two races are also virtually separable by length of maxillary tooththrow. Other cranial measurements (condylobasal length, postorbital constriction, mastoidal breadth) show only slight overlap. Measurements of ear from notch also show little overlap, with *M. r. redmani* being the larger.

*Monophyllus cubanus ferreus* was based upon a series of 24 specimens from the type-locality in extreme southwestern Haiti. Of the type and paratypes, only two were skins, the balance being preserved in spirits. Skins and skulls of *Monophyllus* from Hispaniola are still uncommon in collections, but we have been able to examine one paratype, two freshly taken topotypes, and another individual from central Haiti. The characters of *M. c. ferreus* (in contrast to those of specimens from Cuba) were stated (Miller, 1918, p. 40) to be "color of upperparts clear hair-brown with a slight metallic gloss and with no obvious trace of the buffy-brown or fawn-color characteristic of the Cuban race. Measurements as well as cranial and dental characters apparently identical with those of true *M. cubanus*." Our freshly taken Haitian specimens do not differ appreciably in dorsal color from older (1917-1928) material, but all Hispaniolan specimens are darker (more blackish) than older (1902) specimens from Cuba. A single Cuban *M. r. clinedaphus* collected in 1956 is comparable to older Cuban specimens. The differences in color between bats from

TABLE 1.—*Mensural data for eight populations of Monophyllus showing extremes and means (in millimeters) for five external measurements (bracketed figures= number of specimens included in each calculation if different from N)*

	N	Total length	Tail	Hindfoot	Ear from notch	Forearm
<i>redmani</i>	9 ♀	76.1 (73-80)[14]	9.7 (8-11)[14]	13.0 (11-14)[14]	13.8 (13-14)[4]	40.2 (37.6-41.0)
(Jamaica)	6 ♂					
<i>clinedaphus</i>	17 ♀	65.5 (63-70)[6]	9.5 (8-11)[6]	10.5 (9-11)[6]	11.2 (9-13)[6]	40.1 (38.5-42.8)
(Cuba)	14 ♀					
	1 ♂					
<i>clinedaphus</i>	13 ♂	60.7 (59-60)[3]	10.5 (10-11)[2]	13.0 (11-14)[3]	10.7 (10-11)[3]	39.8 (37.6-42.5)[24]
(Hispaniola)	12 ♀					
<i>portoricensis</i>	10 ♂	65.0 (60-71)	8.3 (7-10)	11.7 (10-13)	11.5 (10-12)[12]	36.9 (35.5-38.5)
(Puerto Rico)	12 ♀					
<i>luciae</i>	4 ♂	73[1]	12[1]	13[1]	-	41.6 (40.1-43.3)
(Anguilla, Barbuda, Antigua)	2 ♀					
<i>luciae</i>	10 ♂	78.1 (69-84)[18]	13.6 (8-16)[18]	14.6 (12-15)[18]	15.7 (15-16)[16]	42.1 (40.6-45.7)
(Dominica)	11 ♀					
<i>luciae</i>	2 ♂		-	-	-	42.1 (40.5-43.7)
(St. Lucia)	11 ♀					
<i>plethodon</i>	2 ♂	67	9	12	14	39.9 (38.8-41.0)
(Barbados)						



TABLE 2.—Cranial data for eight populations of *Monophyllus* showing extremes and means (in millimeters) for six measurements (size of samples as in table 1; bracketed figures = number of specimens used in each calculation if different from N in table 1)

	Greatest length	Condylbasal length	Zygomatic breadth	Postorbital constriction	Mastoidal breadth	Maxillary toothrow
<i>redmani</i> <i>cinedaphus</i> (Cuba)	23.3 (22.8-23.9)	22.0 (21.4-22.6)[14]	9.9 (9.1-10.4)[14]	4.3 (4.2-4.6)	9.7 (9.4-10.0)	8.5 (8.3-8.9)
	21.9 (21.0-22.4)[9]	20.6 (19.7-21.9)[9]	9.2 (8.7-9.8)[9]	4.2 (3.9-4.4)[9]	9.0 (8.9-9.3)[9]	8.0 (7.8-8.3)[9]
<i>cinedaphus</i> (Hispaniola)	21.9 (21.6-22.1)[4]	20.6 (20.2-20.7)[4]	9.3 (8.9-9.7)[3]	4.3 (4.2-4.4)[4]	9.1 (8.6-9.6)[4]	7.8 (7.5-8.0)[3]
	19.9 (19.0-20.4)	18.5 (17.9-18.9)	8.5 (8.2-8.8)[16]	4.0 (3.8-4.2)	8.4 (8.2-8.8)	7.1 (6.8-7.3)
<i>portoricensis</i> <i>luciae</i> (Anguilla, Barbuda, Antigua)	23.4 (22.8-24.0)[5]	22.1 (21.5-22.6)[5]	10.4 (9.8-11.0)[5]	4.8 (4.5-5.0)	9.6 (9.5-10.5)	8.2 (7.8-8.5)
	23.4 (22.8-24.2)[18]	21.9 (21.0-22.5)[18]	10.1 (9.4-10.8)[18]	4.7 (4.5-4.9)[18]	9.8 (9.4-10.5)[18]	8.0 (7.8-8.4)[17]
<i>luciae</i> (Dominica)	23.1 (22.1-23.6)[8]	21.5 (20.6-22.0)[8]	9.9 (9.5-10.2)[8]	4.8 (4.6-4.9)[8]	9.8 (9.5-10.0)[8]	8.0 (7.8-8.2)[8]
	22.3 (21.4-23.2)	20.5 (19.5-21.4)	10.4[1]	4.8 (4.6-5.0)	10.1[1]	7.5 (7.2-7.8)
<i>plethodon</i> (Barbados)						

Cuba and Hispaniola are so slight and depend so much on original treatment and later storage of specimens that we cannot justify the retention of *M.c. ferreus* as a valid subspecies on this basis.

As Miller noted, the Cuban and Haitian populations do not differ in mensural characters. We have available external measurements for only three Haitian specimens and cranial measurements for only four. Although total length indicates a complete dichotomy between Cuban and Hispaniolan specimens (63–70 in Cuba, 59 and 60 in Hispaniola), these data are unreliable because of the small Haitian sample. Extremes of length of forearm for 24 Hispaniolan specimens (37.6–42.5) bracket those of 32 Cuban specimens (38.5–41.8). Cranial measurements of the two populations show identical or similar means, the greatest discrepancy being in length of maxillary toothrow (mean 7.8 in Hispaniola, 8.0 in Cuba). In the latter instance, there are data for only nine Cuban and three Hispaniolan specimens. It is possible that when additional Hispaniolan material becomes available, *M. c. ferreus* can be shown to be a recognizable subspecies, but at this time it appears neither identifiable nor nameworthy.

The recently collected Haitian specimens were taken in a large wet cave in a mesic situation in the Monts Cartaches massif; this cave may well be the same place whence W. L. Abbott secured the holotype and paratypes of *M. c. ferreus* in 1917. Miller (1904, p. 344) reported that William Palmer found this bat abundant on Cuba at the type-locality of *M. cubanus*, a damp cave; Palmer took not only *Monophyllus* but also *Natalus micropus*, *Mormoops blainvillei*, *Pteronotus parnellii*, *Pteronotus macleayi*, and *Phyllonycteris poeyi* at the entrance of this same cave. Allen (1911, p. 231) cited Gundlach's records of *Monophyllus* at Rangel in the Sierra del Rosario in Pinar del Río Province and at Guisa in eastern Cuba. Koopman and Ruibal (1955, p. 3) reported fossil *Monophyllus* from a cave in the Sierra de Cubitas in Camagüey Province, Cuba, and Anthony (1919, p. 637) took a single *Monophyllus* in a cave at Jarahueca, near Sabanilla, in Oriente Province. In Haiti, Miller (1929, p. 8) recorded taking a skull from owl pellet material at Diquini, Département de l'Ouest, and Koopman (1955, p. 110) reported a single fragmentary skull from a cave at Nan Café, Ile de la Gonâve. Presumably this latter specimen is referable to *M. r. clinedaphus* although at least one chiropteran species (*Pteronotus parnellii*) has an endemic subspecies on Gonâve (*P. p. gonavensis*) that differs from its mainland Hispaniolan relative (*P. p. pusillus*). All the above records refer either to fossil or subfossil finds in caves or to cave-taken living bats. Like *M. r. redmani*, *M. r. clinedaphus* is a confirmed cave dweller. We have no data on weights or parturition for *M. r. clinedaphus*.

SPECIMENS EXAMINED.—CUBA: Habana Province: Cueva de Cotilla, 9 km southwest of San José de las Lajas, 3 ♂, 2 ♀ (AS 4776-80); Cueva de la Numancia, Aguacate, 1? (AMNH 176156). Oriente Province: Baracoa, 4 ♂, 2 ♀ (USNM 113668, 113671-73, 113675-76); Cueva de la Majana, Baracoa, 10 ♂, 10 ♀ (MCZ 11658, 16663-65, 16667-69, 16671-73, 16675, 16681, 16684, 16688-89, 16694-95, 16697-98, 16700). HAITI: Département du Sud: Grotte la Forêt, 9 km west-southwest of Jérémie, 6 ♂, 2 ♀ (AS 5599-606); 8 miles west-southwest of Jérémie, 7 ♂, 9 ♀ (USNM 219152-58, 219160-63, 219165, 219167-68, 219171, 219174). Département de l'Artibonite: St. Michel de l'Atalaye, 1 (USNM 253646).

*Monophyllus redmani portoricensis* Miller

*Monophyllus portoricensis* Miller, 1900, p. 34. [Type-locality: cave near Bayamón, Puerto Rico.]

DISTRIBUTION.—Known only from Puerto Rico (see fig. 1).

DEFINITION.—A subspecies of *M. redmani* characterized by small size (total length 60-71, mean 65.0), short forearm (35.5-38.5, mean 36.9), small skull (greatest length 19.0-20.4, mean 19.9) with narrow postorbital and mastoid regions, and narrow zygomata, and short tooththrows. The color is medium brown.

REMARKS.—The subspecies *M. r. portoricensis*, although of about the same body size as *M. r. clinedaphus*, has a distinctly shorter forearm and smaller skull. Greatest length of skull will separate *M. r. portoricensis* (19.0-20.4) from the other subspecies of *M. redmani* (21.0-23.9). Nonoverlap of cranial measurements occurs also in condylobasal length and length of maxillary tooththrow; other skull measurements average smaller, but there is some overlap in these dimensions, the greatest being between *M. r. portoricensis* (high extreme 8.8) and Hispaniolan *M. r. clinedaphus* (low extreme 8.6) in mastoidal breadth. The forearm of *M. r. portoricensis* is distinctly shorter than those of the subspecies *M. r. redmani* and *M. r. clinedaphus*, both of which, despite a discrepancy of body size, have forearms of comparable lengths. Mensural data for 22 specimens of *M. r. portoricensis* are given in tables 1 and 2.

Freshly collected *M. r. portoricensis* seem intermediate in depth of dorsal pigmentation between the darker *M. r. redmani* and the paler *M. r. clinedaphus*. Such color differences are very difficult to assess, owing to the age of the skins involved. The color differences among all subspecies of *M. redmani* are slight at best; verification of supposed differences in pelage among the races must await the availability of fresh specimens from throughout the range of the species.

Anthony (1918, p. 349) commented that *M. r. portoricensis* was uncommon in Cueva de Fari near Bayamón but was the most abun-

dant bat at Cueva de Trujillo Alto. He reported a single fragmentary fossil skull of this subspecies from Cueva Catedral near Morovis, and we have examined a second skull from fossil or subfossil deposits in Cueva de Clara in the same area.

Schwartz and Thomas captured *M. r. portoricensis* in mist nets. Those from near Utuado were collected in a net set in a "cafetal" near the edge of the northern escarpment of the Cordillera Central at an elevation of 1100 feet (336 meters); this area is mesic and heavily forested. At a slightly higher elevation (1300 feet=397 meters) *Monophyllus* was collected near Cidra; here the net was set in a wooded ravine. In the southwestern portion of Puerto Rico, *M. r. portoricensis* was taken from mist nets set in a ravine and across an unused road, both in xeric woods and scrub near sea level. Since the Utuado and Guánica areas represent the two climatic extremes in Puerto Rico, *M. r. portoricensis* seems to tolerate a wide variety of habitats.

We have no data on weights or parturition in *M. r. portoricensis*.

SPECIMENS EXAMINED.—PUERTO RICO: 7.5 km east of Guánica, 1 ♂, 3 ♀ (AS 5526–29); 17.7 km northeast of Utuado, 1 ♂, 1 ♀ (AS 5538–39); Cueva de Trujillo Alto, Trujillo Alto, 3 ♂, 4 ♀ (AMNH 39433–35, 39444–47); Cueva de Fari, Pueblo Viejo, 3 ♂ (AMNH 39430–32); ca. 1 km northeast of Cidra, 1300 ft, 4 ♂, 4 ♀ (AS 5509–12, 5669–70); Cueva de Clara, near Morovis, 1 (KU uncataloged, fossil).

#### *Monophyllus plethodon* Miller

*Monophyllus plethodon* Miller, 1900, p. 35.

DEFINITION.—A species of *Monophyllus* characterized by a combination of large size (total length 67–84), large hind foot (12–15), long forearm (38.8–45.7), large skull (greatest length 21.4–24.2), broad postorbital region (4.5–5.0), and the first and second premolars separated by a diastema much less than half the length of the first premolar. The pelage usually is brown, but a few specimens are pale buffy tan.

#### *Monophyllus plethodon plethodon* Miller

*Monophyllus plethodon* Miller, 1900, p. 35. [Type-locality: St. Michael's Parish, Barbados.]

DISTRIBUTION.—Known only from Barbados (see fig. 1).

DEFINITION.—A subspecies of *M. plethodon* characterized by small body size (total length 67 and 68 in two known specimens), short forearm (38.8–41.0), small skull (greatest length 21.4–23.2), and short tooththrows (maxillary tooththrow 7.2–7.8).

REMARKS.—We are somewhat reluctant to regard the Lesser Antillean *Monophyllus* as comprising two subspecies. It is particularly unfortunate that Barbados is the type-locality of *M. plethodon* since, other than the holotype, we have examined only one specimen from

that island. Measurements of the male holotype of *M. plethodon*, taken for us by Gary L. Ranck, plus those given by Miller (1900, p. 38), show that it is somewhat smaller than the other individual, which was collected in 1961. It is purely on the basis of the holotype that we recognize *M. p. plethodon* as distinct from other Lesser Antillean populations; the second specimen (also a male) has measurements that fall within the parameters established by other Lesser Antillean *Monophyllus*; those of the holotype do not. It is possible that *Monophyllus* from Barbados average slightly smaller than their relatives elsewhere in the Lesser Antilles and, for this reason, we accept *M. p. plethodon* as a distinctive Barbadian subspecies with full cognizance that additional material from Barbados may well demonstrate the incorrectness of this conclusion.

On the basis of the single fresh male examined, there seem to be no differences in color between *M. p. plethodon* and the subspecies *M. p. luciae* that occurs on other Lesser Antillean islands. The recently collected specimen was taken in a mist net set between the buttresses of the road bridge at Jack-in-the-box Gully. The gully is a steep-sided and wooded ravine in an area otherwise devoted to cultivation of sugarcane. *Artibeus jamaicensis* was the only other bat taken in the gully.

SPECIMEN EXAMINED.—BARBADOS: St. Thomas Parish: Jack-in-the-box Gully, 1 ♂ (AS 5302).

***Monophyllus plethodon luciae* Miller**

*Monophyllus luciae* Miller, 1902, p. 111. [Type-locality: St. Lucia.]

DEFINITION.—A subspecies of *M. plethodon* characterized by a combination of large size (total length 69–84), long forearm (40.1–45.7), large skull (greatest length 22.1–24.2), and long tooththrows (maxillary tooththrow 7.8–8.5).

DISTRIBUTION.—KNOWN presently from the Lesser Antillean islands of Anguilla, Barbuda, Antigua, Dominica, and St. Lucia (see fig. 1).

REMARKS.—At the time of its description, *M. plethodon* was compared only with the then-named kinds of *Monophyllus*—*M. redmani*, *M. portoricensis*, and *M. clinedaphus*. The dental peculiarities (primarily the crowding of the upper premolars) used to distinguish *M. plethodon* from these other taxa do indeed distinguish it from these Greater Antillean bats. When *M. luciae* was named (on the basis of 16 specimens), it was compared with *M. plethodon* and was said to differ from the latter in being larger (which apparently it is) and in having less crowded teeth. The teeth of our Barbadian specimen, although crowded as typical of the species, are no more closely appressed than in specimens from St. Lucia, Dominica, or other Lesser Antillean islands. Since there are no skins available from St. Lucia,



we do not know if there are color differences between topotypical *M. p. luciae* and *M. p. plethodon*, but we are inclined to doubt that such occur.

Mensural data for three samples of *M. p. luciae* are presented in tables 1 and 2. External measurements are available only from our large series from Dominica, but comparison with those of isolated bats from other islands indicates no difference in size. Means and extremes of cranial measurements for the three different populations of *M. p. luciae* are quite comparable; some measurements (condylobasal length, zygomatic breadth, maxillary tooththrow) intimate the existence of a cline, with larger bats in the north, but others (greatest length of skull, postorbital constriction, mastoidal breadth) do not demonstrate this phenomenon clearly, if at all. There is no evidence in bats from the northern part of the range of *M. p. luciae* of a trend in size toward the much smaller, geographically adjacent *Monophyllus redmani portoricensis*.

Two specimens of *M. p. luciae* (KU 104779, gravid ♀; USNM 361897, ♀) from Dominica are distinctly paler dorsally than other bats from that island. Instead of being the medium to dark brown of all other *M. p. luciae*, these two bats are pale buffy tan above and only slightly darker (more grayish) below. No other sample of *M. redmani* or *M. plethodon* shows such variation. The mentioned differences in color could be due to dichromatism in the population on Dominica or to change in color of the pelage relating to wear and fading.

*Monophyllus* has not been reported previously from the islands of Antigua and Barbuda. The specimen from Barbuda was collected by P. W. Hummelinck, and his notes state that the bat was found dead near the entrance of Dark Cave. Dark Cave is situated at the bottom of a wooded sinkhole and is about 170 meters long and has three water-filled basins. No other bats of any species were observed in the cave. The four Antiguan *M. p. luciae* were collected in Bat Cave near English Harbour. Both the caves on Antigua and Barbuda are located in xeric regions.

Howes (1930, pp. 102-103) reported taking *Monophyllus* in a cave at Dleau Manioc near the Layou River on Dominica; the cave entrance lay about 200 feet (61 meters) up on the face of cliffs bordering the river. Howes' report of this bat from Dominica has been overlooked by other workers. Of 16 *M. p. luciae* collected by the junior author on Dominica, six were netted in banana groves, four were taken in nets across a trail that separated woodlands from a *Theobroma* grove, and others in a net stretched across part of the Layou River. One individual was netted in a banana grove at Marigot. A male was found dead adjacent to a small cave a few yards from the ocean near

Mahaut. The single specimen taken by the senior author was captured in a mist net stretched across a montane stream in dense rain-forest. Elevations of known occurrence of *M. p. luciae* range from sea level up to approximately 1800 feet (550 meters); these extremes are from Dominica material.

Bats taken in nets that also contained *M. p. luciae* on Dominica include *Artibeus jamaicensis*, *Brachyphylla cavernarum*, *Sturnira angeli*, *Myotis nigricans*, and *Ardops nicholli*. There are no data on associated species from situations wherein *Monophyllus* has been collected on other Lesser Antillean islands.

Females collected on Dominica by the junior author between Mar. 24 and Apr. 22, 1966, were gravid; fetuses varied in length from 17 to 24, with larger fetuses occurring on the later dates. Males during the same period had testes 4 to 4.5 in length. Only one young is born to a female. Weights of males ranged from 13.8 to 17.2; those of females from 12.5 to 17.0, with the single nongravid female weighing the least.

SPECIMENS EXAMINED.—ANGUILLA: Small Fountain Cave, Little Bay, 1 ♀ (AMNH 72367). BARBUDA: Dark Cave, 1 ♀ (RMNH 17854). ANTIGUA: Parish of St. Paul: Bat Cave, 4 ♂ (BMNH 18.4.1.7-9, MCZ 17468). DOMINICA: St. Joseph Parish: Clarke Hall Estate, 100 ft, 7 ♂, 10 ♀ (KU 104766-79, USNM 361896, 391225, 391275); St. Paul Parish: Sylvania, 1 ♀ (USNM 361897); 1½ miles northwest of Mahaut, sea level, 1 ♂ (KU 104780); 6 miles northeast of Roseau, 1100 ft, 1 ♀ (AS 5357); St. Andrew Parish: Marigot, 100 ft, 1 ♀ (KU 104765); St. Lucia: no specific locality, 2 ♂, 11 ♀ (USNM 106090-94, 106098-100, 110901-05).

*Monophyllus plethodon frater* Anthony

*Monophyllus frater* Anthony, 1917, p. 565. [Type-locality: cave (Cueva Catedral) near Morovis, Puerto Rico.]

DISTRIBUTION.—Known only as fossil from Puerto Rico (see fig. 1).

REMARKS.—*Monophyllus plethodon frater* was described from five fragmentary skulls; the species was differentiated from *M. r. portoricensis* by its larger size. Anthony (1918, p. 350) commented:

This large species of *Monophyllus* was apparently contemporaneous with *M. portoricensis* . . . since a typical skull of the smaller *portoricensis* was found in the same deposit with the skulls of *frater*. It is partly for this reason that *frater* has been accorded full specific rank instead of being placed in the line of direct ancestry of *portoricensis* . . . . The relationship with *portoricensis* is very close however and the differences appear to be in size rather than detail. Were the two forms from adjacent islands rather than from the same island doubtless they would best be considered subspecifically related . . . . *M. frater* is probably even more closely related to the larger *M. luciae* from the Island of St. Lucia, Lesser Antilles, than to the small *portoricensis* . . . . Compared with *M. luciae*

the fossil *Monophyllus* may be distinguished by its rather longer rostrum and noticeably longer toothrow.

We have examined three fragments of *M. frater*, including two rostra and one palate. As in other representatives of *M. plethodon*, the diastema between the upper premolars is narrow; the first upper premolar is lacking in the three fragments, but its alveolus and either the alveolus of the second premolar or the tooth itself clearly demonstrate that the two upper premolars were appressed as in the Lesser Antillean *M. plethodon*. There is no question that *M. frater* is related to *M. plethodon* rather than to the Greater Antillean *M. redmani*.

We use a trinomial to show the close affiliations of *M. frater* with *M. plethodon*. There are those who feel that such usage is inappropriate for nonsynchronous taxa. We do so here for three reasons: (1) Although no large *Monophyllus* has been taken in the flesh on Puerto Rico, there is a good possibility that *M. p. frater* may be so encountered. Several other Antillean mammals (*Brachyphylla nana* and *Capromys nana* in Cuba, and *Brachyphylla pumila* on the island of Hispaniola) were named originally from fragmentary cave material and were later secured in the flesh. (2) *Monophyllus r. portoricensis* and *M. p. frater* were apparently at least partially contemporaneous in Puerto Rico, suggesting that the latter species is a relatively recent inhabitant of the island rather than an ancient arrival. Anthony (1918, p. 338), writing specifically about the Cueva Catedral fossils, concluded that "the fossil bats of Cueva Catedral have been fossil for no lengthy period" and that, considering the Puerto Rican fossil fauna as a whole, a "conservative estimate would place the island mammalia as living at the end of the late Pleistocene and there is little doubt that this age may be extended into the Recent." (3) Use of a trinomial clearly shows the close relationship of *M. frater* with the other subspecies of *M. plethodon*. Maintaining two distinct species obscures their obvious affinities.

Anthony's (1918, p. 350) brief comparison of *M. frater* with *M. luciae* (that the former differs from the latter in having a "rather longer rostrum and noticeably longer tooth row") seems to be affirmed by recently acquired specimens of *M. p. luciae* although, considering the total variation in *luciae*, the differences are far from striking. Anthony's measurements (1918, p. 350) of "interorbital breadth" (4.6-4.9 in three *M. frater*) fall within the known variation of our measurements of postorbital breadth in *M. luciae* (4.5-5.0) and above those of *M. redmani* (3.8-4.6 in all subspecies, with *M. r. redmani* most closely approaching the measurements of *M. p. frater*). The alveolar length of the upper molariform series of two *M. p. frater* measures 6.8 and 7.1, quite comparable to similar measurements in other *M. plethodon*. It is even possible that *M. p. frater* is not

worthy of recognition as an entity distinct from *M. p. luciae*. We are deterred from so considering *M. p. frater* by the fact that all skulls are incomplete, usually grossly so, and by the lack of specimens on which pelage characters and external measurements can be ascertained. We therefore retain *M. p. frater* with full knowledge that it may prove later to be synonymous with *M. p. luciae*. Retention of the name at this time permits its convenient use in dealing with the larger of the two species of *Monophyllus* from Puerto Rico.

SPECIMENS EXAMINED.—PUERTO RICO: Cueva Catedral, Morovis, Arecibo, 3 (AMNH 40942-44).

### Discussion

The genus *Monophyllus* is composed of two species, each with three subspecies, which, except for the sympatric occurrence of representatives of each species on Puerto Rico, are allopatric. One species (*M. redmani*) is Greater Antillean in distribution and the other (*M. plethodon*) is Lesser Antillean, except for the occurrence (only in the past?) of a population on the island of Puerto Rico. Such a picture suggests that there have been two independent centers of differentiation of *Monophyllus* in the West Indies with the resultant evolution of two practically allopatric species. The Lesser Antillean *M. plethodon*, however, succeeded in crossing the Anegada Passage and reached Puerto Rico at a time when that island was occupied also by *M. redmani*. Clear evidence of immigration from the Lesser Antilles to the Greater Antilles (in contrast to the reverse situation) is quite rare in the terrestrial vertebrate biota of the Antillean islands, and *M. plethodon* stands out as an invader of the Greater Antilles from the south.

The degree of differentiation of the subspecies of *M. redmani* (in contrast to those of *M. plethodon*) is striking. The races of *M. redmani* (*M. r. redmani*, *M. r. clinedaphus*, *M. r. portoricensis*) all are distinctly different, the primary difference being in overall size and concomitantly in size of skull. Although perhaps interpretable as grossly clinal, with the largest subspecies in the west (*M. r. redmani*) and the smallest in the east (*M. r. portoricensis*), the size difference is not quite so diagrammatically demonstrated as one might assume from first glance. The subspecies *M. r. redmani* and *M. r. clinedaphus*, for instance, have comparably long forearms despite a distinct dichotomy in overall size; secondly, the occurrence of *M. r. clinedaphus* on two islands (Cuba and Hispaniola), rather than each island having its own subspecies, suggests also that we are not dealing with variation of a typically clinal nature.

In contrast to the subspecific differentiation in *M. redmani*, the races of *M. plethodon* are much less distinctly defined. In fact, were



it not for the small holotype of *M. p. plethodon* and temporal considerations of *M. p. frater*, we would be prone to consider *M. plethodon* as monotypic. The limited material of topotypic *M. p. plethodon* and *M. p. frater*, plus the fact that the latter is known only from fragmentary skulls, make assessment of the status of the Barbadian and Puerto Rican subspecies extremely difficult. The geographic isolation of Barbados from the balance of the Lesser Antillean chain and the presence of an apparently isolated segment of *M. p. plethodon* in Puerto Rico have been decisive factors in our retention of these two populations as distinct from the main body of Lesser Antillean *M. p. luciae*. Lack of presently demonstrable differences between the populations of *M. p. plethodon* on the Lesser Antillean islands of St. Lucia, Dominica, Antigua, Barbuda, and Anguilla suggests that the species is relatively stable genetically (a suggestion somewhat confirmed by the small differences among the subspecies *M. p. plethodon*, *M. p. luciae*, and *M. p. frater*), or that there is intercourse between populations of *M. p. plethodon* on the various Lesser Antillean islands (although as yet *Monophyllus* remains unknown from any two adjacent islands except Barbuda and Antigua on the same bank), or that *M. p. plethodon* is a relatively recent arrival on at least some of the Lesser Antillean islands, which it now occupies without sufficient elapsed time for local subspecific differentiation. The latter seems to us to be the most acceptable interpretation. Doubtless, additional collecting will reveal the presence of *M. plethodon* on at least those Lesser Antillean islands (Martinique, Guadeloupe, and the islands of the Anguilla Bank) that lie either between known stations of occurrence of the species or on the same bank as islands from which *M. plethodon* is known.<sup>3</sup> The French islands in particular are poorly explored mammalogically.

The complete dichotomy of *M. plethodon* and *M. redmani* in the one character that distinguishes them—the diastema between the upper premolars—makes any analysis of relationships, history, and loci of origin extremely difficult. The general concordance in size of *M. plethodon* and *M. r. redmani* suggests that the latter is the subspecies of *M. redmani* most closely related to *M. plethodon*. This indeed may be the case, but *M. r. redmani* occupies that island (Jamaica) in the range of the species that is farthest removed from the present distribution of *M. plethodon*. Perhaps *M. r. redmani* was an early fortuitous arrival in Jamaica from the Lesser Antilles. Data presented by Koopman and Williams (1951), however, suggest that *M. redmani* arrived relatively recently on Jamaica although Williams (1952)

<sup>3</sup> After this paper was submitted for publication, a specimen of *M. plethodon* was collected on St. Vincent by a field party from the Museum of Natural History, University of Kansas.



reported finding *Monophyllus* as a fossil on the island. Absence of *Monophyllus* from earlier Jamaican fossiliferous deposits may be due merely to the chance nature of such deposits themselves.

Once established on Jamaica, *M. redmani* could thus have extended its distribution to Hispaniola (*M. r. clinedaphus*) and still further to Puerto Rico (*M. r. portoricensis*). Since Hispaniola and Cuba both are inhabited by *M. r. clinedaphus*, we suggest that Cuba was the last island of the Greater Antilles to be invaded by *Monophyllus*, that these invaders came from Hispaniola to the east rather than from Jamaica to the south, and that there has been little or no subsequent divergence of the Cuban populations of *M. r. clinedaphus* from their Hispaniolan forebearers.

Meanwhile, in the Lesser Antilles, *M. plethodon* became established on some of the Windward Islands from a center of origin there. Any of the mountainous inner chain of islands would seem a suitable locus for the origin and center of dispersal of *M. plethodon*: Dominica or Guadeloupe, both near the central portion of the Lesser Antillean arc, might have been the region whence *M. plethodon* colonized the balance of these islands. From this Lesser Antillean center, *Monophyllus* reached Barbados (*M. p. plethodon*) on one hand and Puerto Rico (*M. p. frater*) on the other, while the parent populations (*M. p. luciae*) remained in situ on the Windward and Leeward Islands. Although this suggested history may bear little resemblance to the sequence of events as they really occurred, it offers at least a tentative explanation that appears to do little violence to the relationships and distribution as currently understood.

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### Dominica Survey in the *Proceedings*

paper	author	subject	year	volume	number
1	Kier	Echinoids	1966	121	3577
2	Stone	Diptera: Anisopodidae, Bibionidae	1966	121	3578
3	Kirsteuer	Marine archiannelids	1967	123	3610
4	Allen	Hymenoptera: Tiphidae	1967	123	3617
5	James	Diptera: Stratiomyidae	1967	123	3622
6	Jones and Schwartz	Bats of genus <i>Ardops</i>	1967	124	3634